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INSECT SUCCESSION IN THE DECOMPOSITION OF A MAMMAL IN COSTA RICA[1]

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Abstract.—Observations were made on the decomposition of a dead dog during the dry season of 1977 in the Central Valley of Costa Rica, Central America. The terrain is classified as premontane humid forest and the observations were made in a secondary forest. The general pattern of decomposition was basically the same as has been described by authors in other latitudes, but different in the ecological complexity and the insect fauna involved. The classification used for human cadavers by forensic pathologists in Costa Rica and other countries in the American tropics was utilized in this study. It includes the following stages: discoloration, emphysematic (bloated), liquefaction and skeletal remains. The succession of different species appeared to depend on their specific feeding preferences, interspecific competition, and the microclimate provided by the substratum. Marked changes in the activity of populations during crepuscular periods coincided with an increase in relative humidity and a decline in temperature in the macroenvironment of the surrounding forest. Included among the principal insect consumers of the remains were the calliphorid dipterans *Phaenicia eximia* Wiedemann and *Hemilucilia segmentaria* Fabricius, the piophilid dipteran *Prochyliza azteca* McAlpine and the coleopteran *Dermestes carnivorus* Fabricius. The most important predators were the histerids *Euspilotus aenicollis* Marshall, *Hister punctiger* Paykal and *Geomysaprinus* (*Priscosaprinus*) *belioculus* Marshall. Some of these species have also been associated with a similar type of substratum in the tropical rain forest and tropical dry forest in Costa Rica.

Introduction

Much is known about the behavior and taxonomy of the principal groups of insects that participate in the successional stages of decomposition in temperate zones, but relatively few studies have been made in tropical zones (Bohart and Gressit 1951; Cornaby 1974; Payne 1965). Previous studies have shown that certain general patterns exist during the decomposition process that accounts for the natural or slightly altered ecological conditions. The decomposition phenomenon, although it presents a continuum of changes, has been divided into various phases or stages in order to facilitate its study

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(Johnson 1975; Payne 1965; Reed 1958). Given the limited knowledge of this process in the neotropical region, the objective of our study was to interpret and characterize the decomposition process in a dead dog, and to determine the principal insect species that were present.

Materials and Methods

Field observations were made during the dry season of 1977 in a secondary forest on the campus of the University of Costa Rica, in San José, Costa Rica, Central America. The altitude of the study area is 1,200 m. The substrate utilized was a dead female dog that had been euthanized with nembutal (Pentobarbital). The carcass was placed on the floor of the forest and observations were made each day for 28 days, every four hours from 0600 hours to 1800 hours with an additional observation at 2000 hours. From the 28th through 48th day, observations were made every 4th day, and subsequent observations were made on days 58, 70, 80 and 90. At each observation period, recordings on temperature, relative humidity, state of decomposition of the dog, dominant insect population and predation were made. Samples of adult and larval insects were collected for later identification. Larvae were reared to the adult stage for identification. Particular attention was given to the collection of the most abundant species. Rarer species were grouped according to the similarity of their ecological function and identified only to family level.

Results and Discussion

Our observations indicated that decomposition in the tropics has the same general pattern as described for temperate zones. The differences are principally in the number and duration of the phases, the insect faunae involved and the degree of ecological complexity (Johnson 1975; Payne 1965; Reed 1958). In our study we utilized the classification used by forensic pathologists in Costa Rica and other Latin American countries for human cadavers (López and Gisbert 1962; Vargas 1977). This classification divides the decomposition process into four phases as follows:

Discoloration.—Color changes begin immediately following death and include pallid color of the lips, nose, feet and abdominal region and green color of superficial veins. Hobson (1932) found that during this initial period the tissues are acid and not suitable for feeding by fly larvae, which feed on the liquid between muscle fibers. Later, the tissues become alkaline, the sarcolemma dissolves and the intermuscular tissue is attacked by the larvae. In our study this phase lasted approximately three days (Fig. 1). During this period we observed the presence of ants (*Camponotus* sp.), muscoid, sarcophagid and drosophilid flies and a large number of the calliphorid, *Phaenicia eximia* Wiedemann, which oviposited in the throat region near the nasal fosae, and in the eyes, mouth, vagina and anus.

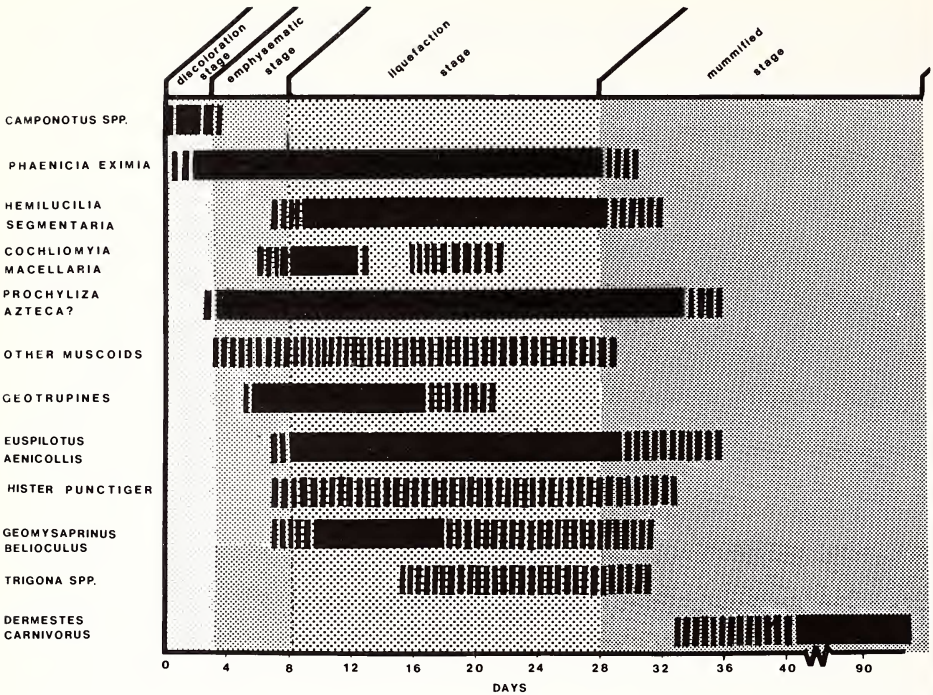

Fig. 1. Appearance of insect populations thru the necrologic stages of decomposition of a dead dog in the Central Valley of Costa Rica, during dry season of 1977. ■ High population density, |||| low population density.

Emphysematic state.—This state of degradation is characterized by marked tumefaction of the abdomen and other body regions and protrusion of the eyes and tongue. This condition is caused by anaerobic decomposition of the proteins and is subject to individual variation (Johnson 1975; Payne 1965; Reed 1958). Duration of this period is variable and probably depends on the temperature and other environmental conditions.

In this study, this phase lasted approximately four days. During this time the main insects observed were large foci of active larvae in the anal and mandibular regions. The majority of the specimens collected from these two regions were *P. eximia*. At night, adults of the histerid beetle *Euspilotus aenicollis* Marshall, and certain geotrupine scarabs comprised the majority of the active faunae. This group of Coleoptera hid during daylight hours in holes dug into the soil near or beneath the body of the animal. Similar behavior was also observed by Payne (1965) in the temperate zone. During the final part of this phase, bare areas developed near the soil interphase due to hair slippage. Several muscoid flies were observed ovipositing on these fleshy exposed regions.

Liquefactive stage.—This stage is characterized by the liquefaction of the

viscera and soft tissues. It begins with breakage of the skin in one or more places, permitting entry of air and leading to aerobic decomposition (Reed 1958). Johnson (1975) interpreted this phase as a general deterioration of the tissues until only dried tissues and bones remained, with a loss of 90 percent of the original weight of the carcass. This degenerative phase corresponded to what Payne (1965) divided into two steps: active decay stage and advanced decay stage.

In the present study, this phase began on the 8th day and lasted approximately 19 days. During this phase we observed the greatest activity by necrophilic insects, both in the size of population present and the variety of species.

In the initial part of this phase we observed that the remains of the animal underwent rapid deterioration. Muscoid fly larvae of various species, in various stages of development, constituted the most conspicuous group of insects, but the majority of the pupae collected were of *P. eximia,* the pioneer species. It is important to note that this calliphorid completed two or perhaps three generations during degradation of the carcass, and, together with *Hemilucilia segmentaria* Fabricius and the piophilid *Prochyliza azteca* McAlpine were the most abundant species during this phase of decomposition. Adult insects, including silphids and other Coleoptera were observed but not identified to species level.

The abundance of fly eggs and larvae attracted numerous predators. These were most abundant at night and included staphylinids, and especially histerids (*E. aenicollis, Hister punctiger* Paykal, and *Geomysaprinus* (*Priscosaprinus*) *belioculus* Marshall). Other species occasionally observed included dermapterans, an ichneumonid, some forest roaches, wasps (probably of the genus *Stelopolybia*), bees of the genus *Trigona* and lepidopterans (Pyralidae and Noctuidae), none of which were identified to species.

After twelve days there was a marked decline in the population of adult muscoids visiting the carcass, although larval activity was still very intense. We observed an increase in the quantity of pupae in the soil around the remains of the animal. A new focus of larval activity occurred in the thoracic region, which included larvae of *P. eximia, H. segmentaria* and *Cochliomyia macellaria* Fabricius. At night, histerids and certain staphylinids were the most abundant predators.

After twenty days, the remains of the dog were dehydrated and the dynamics of the decomposition process began to slow. Activity of the larvae of the necrophilic species was reduced and they began to migrate to the

[3] On the 18th day we observed a recent human fecal deposit 15 meters from our study material. Insects attracted to the feces included adult sarcophagid, muscid and calliphorid flies with *C. macellaria* and *P. eximia* the most abundant species, although as noted above, they were absent as adults on the remains of the dog at this time.

lower and internal areas where moisture content was higher. Emergence of adult forms, which began on the 18th day became more marked. Histerids, staphylinids and some dermestids (this latter group had recently appeared) were active in the same areas in which fly larvae were found.

During the following days the process of dessication became more accentuated and larvae of calliphorids and other groups were restricted to small more liquid zones. Recently emerged adults left the area. Numbers of *P. azteca* and other small dipterans that had been constantly present during most of the degradation process also diminished considerably. Populations of predators during the final part of the liquefactive phase were eventually limited to the histerids, *E. aenicollis, H. punctiger* and *G. belioculus*. Visits by bees of the genus *Trigona* became most frequent as they collected material for construction of their nests (Wille 1965).

Mummification.—The process of decomposition was virtually interrupted in the liquefactive phase. Instead of continuing to a state termed "skeletal remains" by forensic pathologists, however, a process of mummification began. This phenomenon occurs frequently in tropical zones under conditions of low humidity, high temperature and appropriate air circulation (Vargas 1977).

During our study period (1–28 February 1977) there was no rain, and warm air circulated over vegetational cover of the forest, contributing to a high degree of mummification of the remains. A large proportion of the muscle tissue dried and became hard, principally those areas in direct contact with the sun's rays. However, it was possible to observe a few larvae and pupae of muscoid flies in these lower zones that were in contact with the soil.

On the thirty-second day we began to observe the presence of adult dermestids (which had disappeared many days before) and on the fortieth day there appeared the first larvae of *Dermestes carnivorus* Fabricius, which later increased to high population levels. These larvae constituted the dominant population at least until approximately day ninety. The remains were consumed by the larvae of this coleopteran through the skeletal phase at the end of the dry season, when our observations ceased.

Temperature and humidity.—The effects of temperature and humidity on the behavior of populations of necrophilic insects have been observed by various authors. Reed (1958) did not note appreciable changes in the activity of necrophilic insects during periods of rainfall, while Payne (1965) stated that the activities of insects involved in the putrefactive process were influenced more by temperature than by other environmental factors.

We observed a marked change in the activity of larvae and adults at the beginning and end of daylight period. During our initial 28 day observation period, diurnal temperature was relatively constant, ranging from 18.5°C to 20°C between 0600 hours and 2000 hours. During the night, relative humidity was usually 100% and temperature about 15°C.

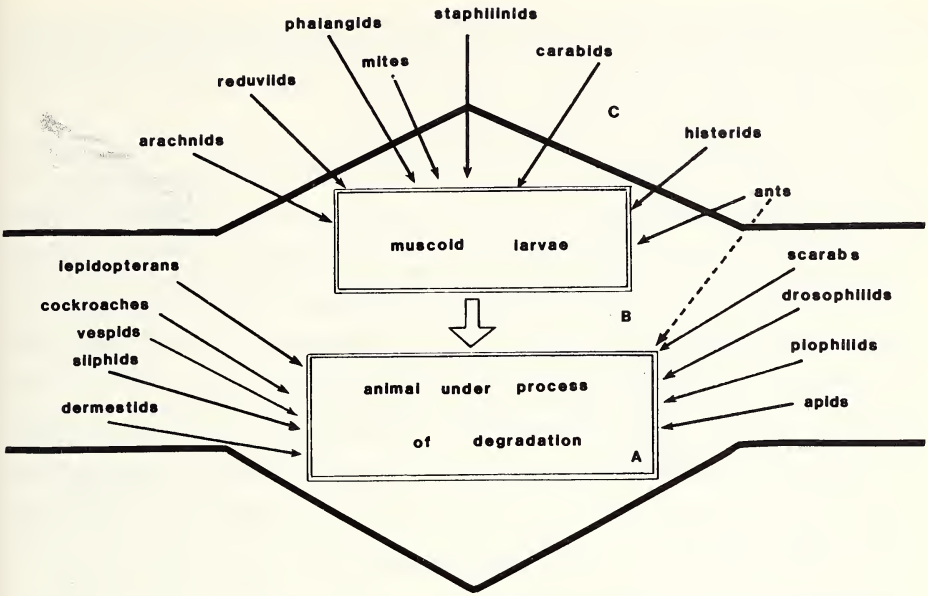

Fig. 2. Trophic relationships observed among arthropods associated with the carcass of a mammal in a premontane humid forest. Trophic levels: A. animal under process of degradation, B. Primary consumers, and C. Predatory insects.

During the dry season temperature and humidity are relatively stable during daylight hours. However, atmospheric conditions are less stable during the rainy season in the Central Valley of Costa Rica. During the months of October and November of 1974 (rainy season) one of us (L. F. J.), working in a preliminary study in the same forest, observed a clear reduction in the activity of adult and larval muscoid flies associated with a dead armadillo (*Dasypus novemcinctus*) on cold cloudy days.

Feeding relationships.—Trophic levels associated with the decomposition of the vertebrate comprised three categories (Fig. 2). The first level was comprised of the material undergoing degradation by bacteria and fungi. The second level was comprised of primary consumers including larval and adult coleopterans, principally of the families Silphidae, Scarabaeidae and Dermestidae and dipterans of the families Calliphoridae, Drosophilidae, Chloropidae, Otitidae, Piophilidae, Phoridae and Sarcophagidae. Other primary consumers included certain Hymenoptera, Lepidoptera and roaches that occasionally fed or extracted material from the substrate. The third level was comprised of secondary consumers that were predators of the primary consumers. These predators were principally histerids, staphylinids, vespids, ants, phalangids, chilopods and reduviids. In the primary study mentioned above, during the rainy season we observed a greater variety of

secondary consumers which included practically the same groups as seen during the dry season plus other arthropods: carabids, spiders, abundant mites *Macrocheles muscadomesticae* (Scopoli) and a braconid mycrohymenopteran which was a parasite of fly pupae.

Appreciable differences in the time of appearance of the different necrophilic species were observed during the process of decomposition (Fig. 1). The presence and abundance of a given species appeared to depend largely on its microclimatic and feeding tolerances and preferences. There was not a strict relationship between a given decompositional stage and the presence of any particular species. For example, the piophilid *P. azteca* was present for many days, independent of the stage of decomposition, probably because this insect feeds on secretions and exudations of the carcass, and its environmental and feeding preferences are apparently wide. The presence and abundance of larval and adult stages of a given insect varied. For example, the calliphorid *P. eximia* was present for a long period of time, although the adults were not attracted to the carcass after the second half of the liquefactive phase. However, they and other muscoid flies were present in the area as was evidenced by attraction to fresh human feces in the vicinity.

Temperate zone studies have shown seasonal variation in the occurrence of muscoid species in carcass substrates (Johnson 1975; Reed 1958). Denno and Cothran (1975) indicated that in addition to seasonal variations, the size of the carcass and intraspecific competition among the necrophilic insects influence the presence of fly species. We found that some calliphorid species occur throughout the year in the tropics, although there may be variations in population densities related to season of the year and the types of substrates available (Cornaby 1974; Jirón 1979).

The presence of *Dermestes carnivorus* also appears to depend on the biochemical condition of the carcass and on the microclimate. Favorable conditions for development of large dermestid populations were present after the cessation of the liquefactive phase, when large portions of the carcass began to dry. The absence of rain also appears to favor the presence of this coleopteran, which was present for several weeks in the dried carcass. This requirement for dry conditions may explain the fact that dermestids appear sporadically during the liquefactive phase and later disappear, before reappearing in the mummification stage.

The presence of the predators *H. punctiger, E. aenicollis, G. belioculus* and others depends mainly upon the abundance of fly larvae, microclimatic conditions, and probably interspecific competition. State of decomposition in the carcass did not affect these predatory insects directly. It is important to note that several of the principal species observed in our study in the Central Valley of Costa Rica (premontane humid forest) were observed also by Cornaby (1974) in tropical humid and tropical dry forest of the same country. Also the calliphorids *P. eximia, H. segmentaria* and *C. macellaria*

have been found associated with human cadavers in the liquefactive stage in several regions of Costa Rica (Jirón 1979).

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